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The copepodid and two chalimus stages of *Caligus latigenitalis* Shiino, 1954 (Copepoda, Siphonostomatoida, Caligidae), parasitic on Japanese black sea bream, *Acanthopagrus schlegeli*

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ABSTRACT The copepodid, the second chalimus, and both sexes of the fourth chalimus of *Caligus latigenitalis* Shiino, 1954 are described based on specimens obtained together with adults from black sea bream *Acanthopagrus schlegeli* cultured in Hikimoto, Japan. No developmental stages of *C. latigenitalis* have been described thus far. The chalimus larvae of this species could be identified to stage, and the stages confirmed, by the basal structure of the frontal filament and the body length as compared to some congeners. The following points are discussed: quantitative variation of armature elements of the legs among congeneric copepodids, growth increments in the successive chalimus stages, the two types of frontal filament recognized among congeneric chalimus larvae, and the problematic, so-called preadult stage. The number of postnaupliar developmental stages is deduced to be six, the same as in other copepod groups including the free-living forms.

KEY WORDS parasitic copepod / *Caligus* / *Acanthopagrus* / black sea bream / chalimus stages

Introduction

The recent redescription of *Caligus latigenitalis* Shiino, 1954 was based on adults (Izawa & Choi, 2000). Here, the copepodid, the second chalimus, and both sexes of the fourth chalimus of this species, i.e. a discontinuous series of stages, are described based on specimens collected together with adults from the body surface of cultured black sea bream, *Acanthopagrus schlegeli*. Developmental stages of *C. latigenitalis* have been unknown thus far.

In the genus *Caligus* Müller, 1785 the copepodid (the first copepodid) succeeding to two nauplius stages is the last free-swimming larva and the infective stage, as in many other groups of parasitic copepods. The ability to swim is indispensable for the copepodid to seek a host, and thus its fundamental structure is comparable even with copepodids of free-living copepods. The chalimus stages following the copepodid are, however, a characteristic phase of caligid copepods. There are four chalimus stages (Gurney, 1934; Kabata, 1972; Boxshall, 1974; Kim, 1993), which are attached to the host by means of a frontal filament. During these stages degeneration of the body structure occurs first and then reconstruction and growth toward the adult proceed gradually. Identification of chalimus larvae to stage involves some difficulties, especially in discontinuous specimen series, because these larvae are flabby and the discriminative features of each stage are not necessarily clear. However,

lately, from a detailed study of the frontal filaments of the chalimus larvae of *C. elongatus* von Nordmann, 1832, Piasecki & MacKinnon (1993) showed that the proximal structure of the frontal filament serves as a stage indicator of the chalimus. Kim (1993) simultaneously reported the same in *C. punctatus* Shiino, 1955 and showed that the identification of chalimus stages could be further confirmed by the discrete size ranges of successive stages. The chalimus larvae of *C. latigenitalis* have the same type of frontal filament as those seen in *C. elongatus* and *C. punctatus*. Based on comparisons with these species, identifications of chalimus stages in *C. latigenitalis* are thus confirmable.

In the discussion the following points of potential relevance to systematics and comparative ontogeny will be addressed: quantitative variation of the armature elements of the legs among congeneric copepodids, growth rate in the chalimus stages, the two types of frontal filament recognized among congeneric chalimus larvae, and the problematic, so-called preadult stage.

Materials and Methods

One copepodid and three chalimus larvae of *Caligus latigenitalis* Shiino, 1954 were collected together with 72 adults from the body surface of black sea bream, *Acanthopagrus schlegeli*, cultured in Hikimoto, Mie Prefecture, Japan, on 1 August 1975. The specimens, fixed in formalin and preserved in alcohol, were examined in lactic acid with a differential interference contrast microscope (Olympus BH-2) using the wooden slide technique of Humes & Gooding (1964). Drawings were made with the aid of a drawing tube. The terminology is based on Kabata (1979) in general and Piasecki & MacKinnon (1993) for the structure of the frontal filament of the chalimus larvae.

Description of Developmental Stages

Copepodid (Figs. 1A-2B)

Body composed of cephalothorax and four-segmented postsome. Body 0.55 mm long excluding caudal rami. Cephalothorax 0.34 mm long on midline, comprising 62% of body length, and 0.23 mm wide. Postsome 0.21 mm long excluding caudal rami, comprising 38% of body length, and 0.10 mm wide at second pediger. All postsomal somites wider than long. Sensory hairs present on lateral margin of cephalothorax at about midlength and on dorsal surfaces of second and last postsomal somites (Fig. 1A, C). Eyes and frontal gland seen in anterior half of cephalothorax through cuticle. Caudal rami wider than long, each armed with six subequal pinnate setae.

Antennule (Fig. 1B, D) two-segmented, about 0.1 mm long excluding setae. Formula for armature elements of segments 3, 9 + 2 aesthetascs; two long terminal setae bifurcate at base with each branch subdivided apically; one subterminal seta bifurcate at about its midlength. Antenna (Fig. 1B, E) three-segmented; basal segment stumpy and

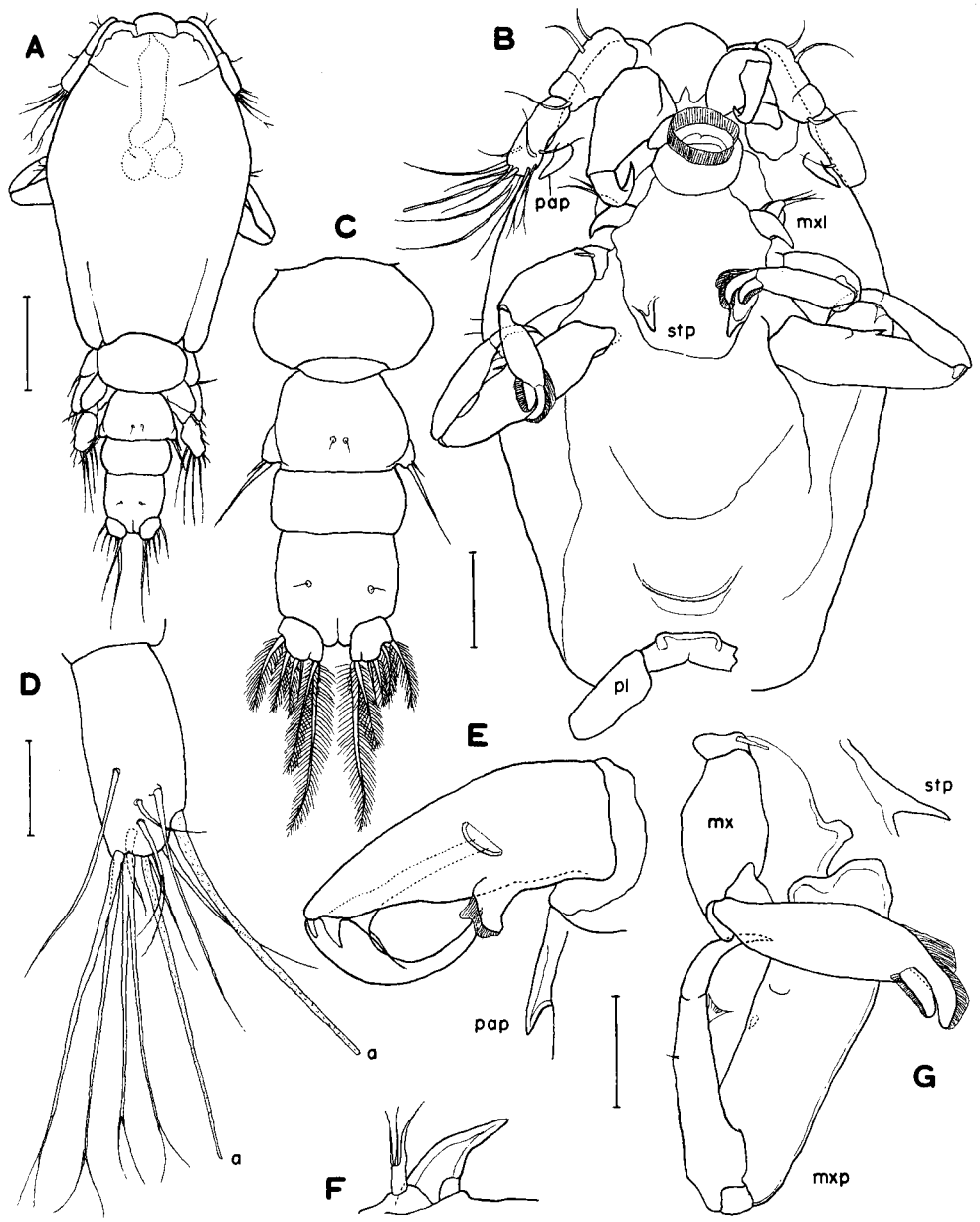

Fig. 1. *Caligus latigenitalis* Shiino, 1954, copepodid. A, habitus, dorsal; B, cephalothorax, ventral; C, metasome and urosome, dorsal; D, terminal segment of antennule, ventral; E, right antenna and postantennary process, medial; F, maxillule, lateral; G, right maxilla, maxilliped and sternal process, ventral. Abbreviations: a, aesthetasc; mx, maxilla: mxl, maxillule; mxp, maxilliped; pap, postantennary process; stp, sternal process. Scale bars: 0.1 mm for A, 50 μm for B,C; 20 μm for D; 30 μm for E, F, G.

almost fused with sternal plate; middle segment 90 μm long, robust, tapered distally, furnished with membrane-fringed, terrace-like expansion on posterior side and ridge-like sclerite on medial side at about midlength, with internal tendon-like structure connecting latter to terminal segment; terminal segment in form of curved hook with basal seta, about half as long as preceding segment, tip of hook meeting expansion of middle segment to form subchela. Postantennary process (Fig. 1B, E) with sharp point. Maxillule (Fig. 1B, F) comprising sharply pointed process accompanied by papilla bearing three setae. Maxilla (Fig. 1B, G) three-segmented, about 0.12 mm long, brachiform; basal segment very short, with feeble membranous tube representing orifice of maxillary gland on anterior margin; middle segment about 50 μm long, unarmed; distal segment about 70 μm long, armed with two membtane-lined, digitiform terminal processes. Maxilliped (Fig. 1B, G) two-segmented, proximal segment stout, about 0.11 mm long, with small spine-like process and indistinct scaly process on medial side at about midlength; distal segment about 80 μm long including claw, tapered distally to pass curved claw, with finletlike membrane mediodistally and spinule at about distal one-third of outer side. Paired sternal processes sharp, located between and slightly anterior to bases of maxillipeds.

First and second swimming legs (Fig. 2A, B) biramous, consisting of two-segmented protopod and unimerous rami. Formula for spines (Roman numerals) and setae (Arabic numerals) on legs as follows:

Leg 1 Protopod 0-0; 1-0 Exopod I,III,4 Endopod 7
Leg 2 Protopod 0-0; 1-0 Exopod I,II,4 Endopod 6

Outermost seta of exopod with membrane along outer side and pinnate on inner side in both legs.

Second chalimus (Figs. 2C-3D)

Frontal filament missing. Body (Fig. 2C, D) flattened dorso-ventrally, 1.11 mm long excluding caudal rami and 0.75 mm wide. Cephalothorax including postmedial lobe ovoid, longer than wide, 0.91 mm long and comprising 82% of body length. Postmedial lobe with shallow posterolateral sinuses, wider than long, 0.25 x 0.40 mm, delimited from anterior portion of cephalothorax by suture. This portion consisting of second and third pedigerous somites. Postsome (Fig. 2E) 0.20 mm long excluding caudal rami, indistinctly three-segmented and attenuated distally, consisting of fourth pedigerous somite, genital complex with small posterolateral processes representing rudimentary fifth legs, and abdominal somite. Caudal rami indistinctly separated from abdominal somite, wider than long, each with six setae on distal margin, longest seta pinnate.

Antennule (Fig. 2F) about 0.15 mm long, indistinctly three-segmented; proximal segment naked, middle segment with seven setae on anterior margin, distal segment with eight setae and one aesthetasc, all setae simple. Antenna (Fig. 2G) reduced in size, about 60 μm long, distinctly smaller than antennule, two-segmented; proximal segment stumpy, unarmed; distal segment depressed, with two, respectively hooklike and digitiform processes and small seta. Postantennary process absent. Oral cone, mandible, and maxillule (Fig. 2H); mandible with about 9 teeth; maxillule in form of stout triangular process accompanied by

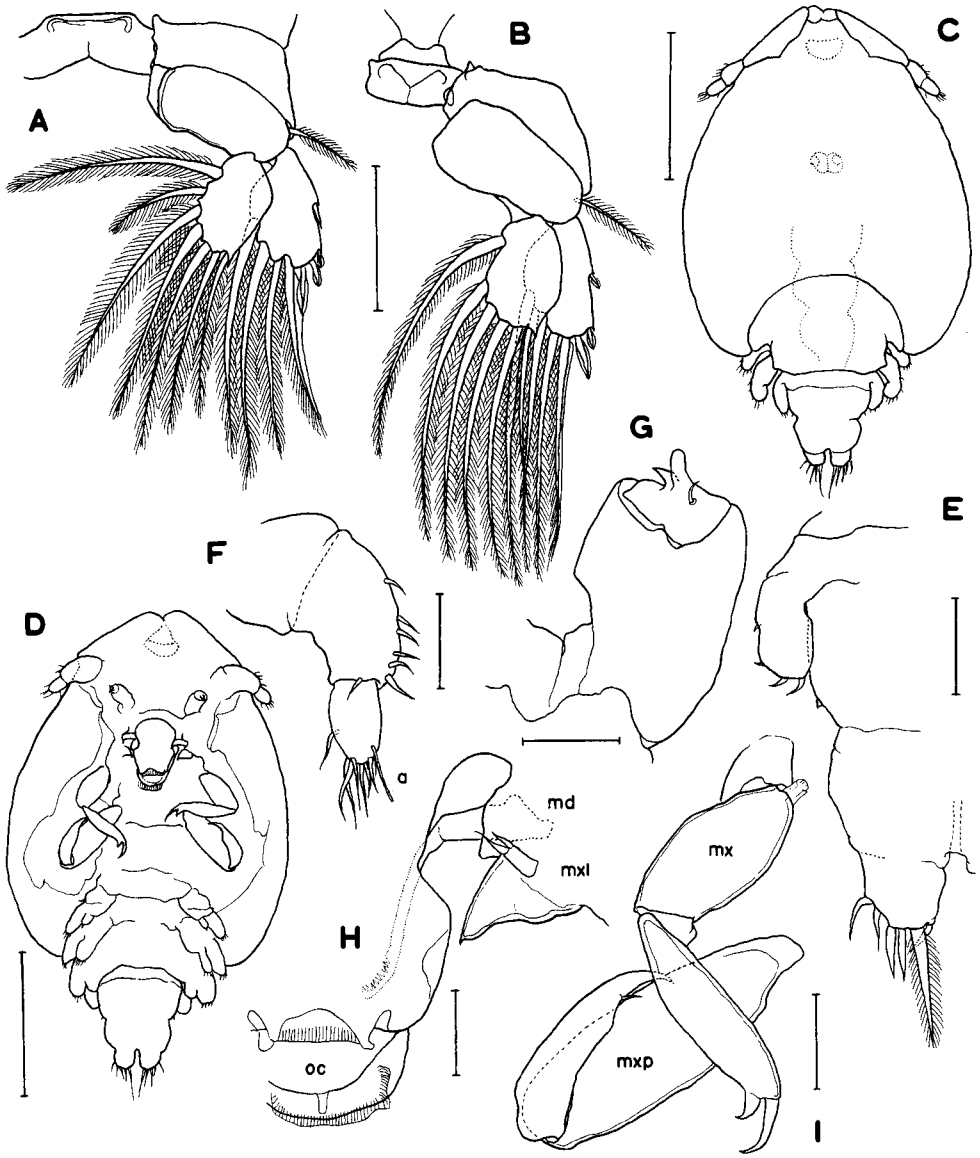

Fig. 2. *Caligus latigenitalis* Shiino,1954, copepodid (A, B) and chalimus 2 (C-I). A, first leg, ventral; B, second leg, ventral; C, habitus, dorsal; D, same, ventral; E, urosome, ventral; F, antennule, ventral; G, antenna, lateral; H, part of oral cone and left mandible and maxillule, ventral; I, right maxilla and maxilliped, ventral. Additional abbreviations than those in Fig. 1: md, mandible; oc, oral cone. Scale bars: 50 μm for A, B, E, F, I; 0.3 mm for C, D; 30 μm for H; 20 μm for G.

pappila bearing two setae. Maxilla (Fig. 2I) about 0.25 mm long, three-segmented; first segment short with opening of maxillary gland, second segment slightly shorter than third one, terminal claws lacking membranes. Maxilliped (Fig. 2I) almost as long as maxilla, two-segmented, second segment with seta on base of terminal claw instead of membrane of copepodid.

First three legs (Fig. 3A, B, C) degenerative, segmentation indistinct, biramous with unimerous rami. Leg 4 (Fig. 2D) lobate, with three elements. All armature elements of four pairs of legs feeble, simple, and short. Setation formula of first three legs as follows:

Leg 1	Protopod 1-1	Exopod 1,6,1	Endopod 1
Leg 2	Protopod 1-1	Exopod 1,7,1	Endopod 7,1
Leg 3	Protopod 1-1	Exopod 1,6	Endopod 4,1

Fourth chalimus (Female, Figs. 3F, J, 4F; Male, Figs. 3E, G, I, K; 4A-E).

Female (Fig. 3F) and male (Fig. 3E) almost same in size and shape, but distinguished by sexually dimorphic antennae and rudimentary legs on genital complex. Proximal portion of frontal filament with three extension lobes and two pairs of connecting pads in both sexes.

Body length 2.45 mm in female, 2.32 mm in male; carapace 1.89 mm long, 1.61 mm wide in female, 1.82 mm and 1.66 mm in male, respectively. Carapace comprising about 79% of body length in both sexes. Postsome consisting of fourth pedigerous somite, genital complex, and one-segmented abdomen in both sexes. Caudal rami wider than long, bearing three pinnate and three short setae each. On genital complex, female with rudimentary fifth legs, each represented by three setae on posterolateral border (Fig. 4F); male with rudiments of sixth legs as well, each represented by two setae in addition to those of fifth legs (Fig. 4E).

Female specimen advanced, with lunules and sternal furca of next, adult stage visible internally through cuticle. Sternal furca seen beneath intercoxal plate of leg 1 (Fig. 3L), and pair of sclerotic nodules regarded as forerunner of sternal furca visible on sternal surface just anterior to intercoxal plate (Figs. 3L, 4A).

Antennule (Fig. 3H) mounted on short pedestal, two-segmented; first segment bearing 24 setae on anterior margin, almost all of which plumose, second segment with seven simple setae and one aesthetasc. Antenna (male, Fig. 3I; female, Fig. 3J) three- or four-segmented, segmentation indistinct proximally, accompanied posterolaterally to basal portion almost fused with sternal surface by hook-like postantennary process. Penultimate segment longest, unarmed in both sexes. Terminal segment forming stout claw in female, but in male knoblike with two small setae and minute apical point. Postantennary process accompanied proximally by three papillae with sensory hairs. Mouth-parts through maxilliped basically same as in second chalimus. Maxilla (Fig. 3K) two-segmented, with opening of maxillary gland at base, with one additional short spine at distal one-third on anterior side.

First three legs (Fig. 4A, B, C) biramous, with two-segmented protopod and two-segmented rami except for degenerative endopod of first leg. Formula for spines (Roman

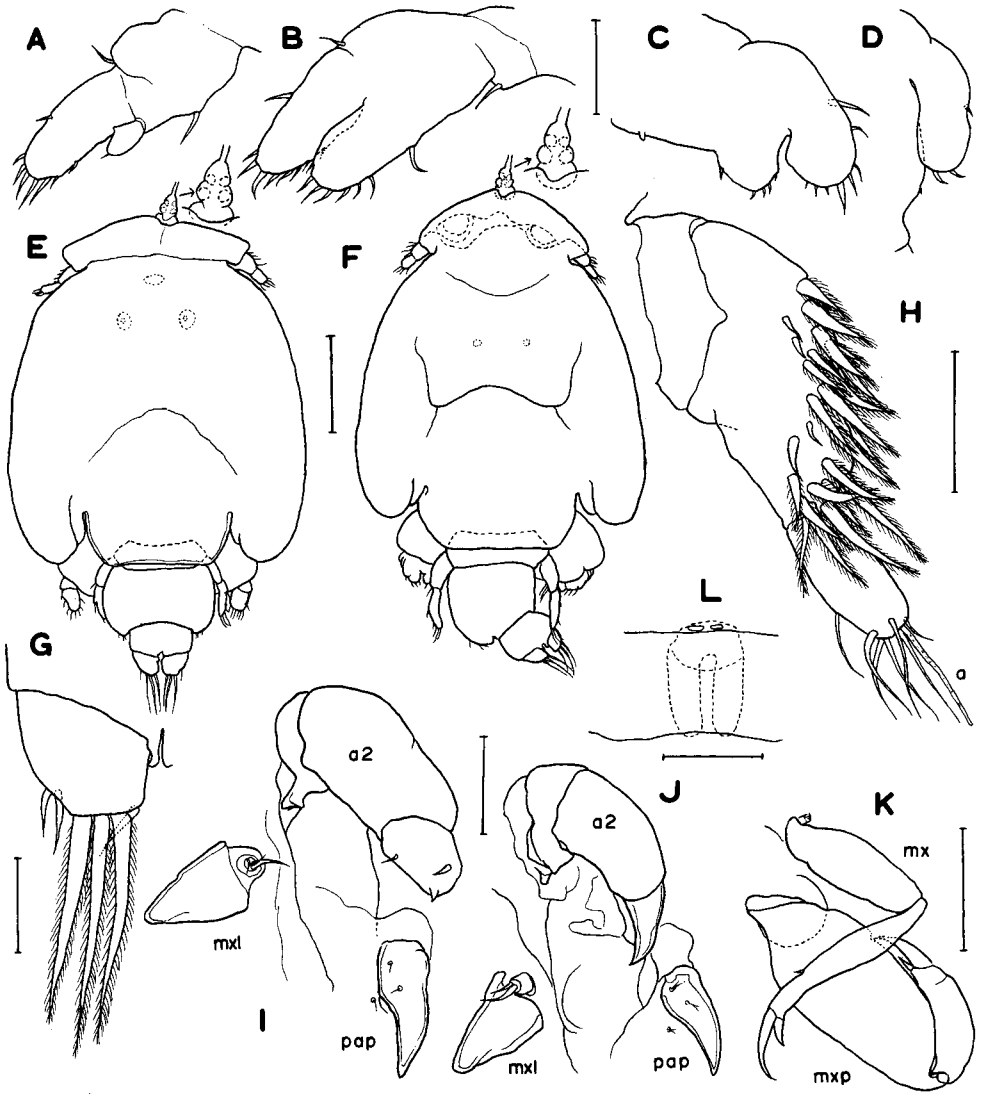

Fig. 3. *Caligus latigenitalis* Shiino,1954, chalimus 2 (A-D) and chalimus 4 (female, F, J, L; male, E, G-I, K). A-D, first to fourth legs of chalimus 2, ventral; E, chalimus 4 male, dorsal; F, chalimus 4 female, dorsal; G, caudal furca of male, ventral; H, antennule of male, ventral; I, left antenna, maxillule, and postantennary process of male, ventral; J, same portion of female, ventral; K, maxilla and maxilliped of male, L, forerunner of sternal furca and intercoxal bar of first leg, sternal furca of next stage seen through cuticle, female, ventral. Additional abbreviation beyond those in Figs. 1 and 2: a2. antenna. Scale bars: 50 μm for A-D, 0.5 mm for E, F; 0.1 mm for G-J, L; 0.2 mm for K.

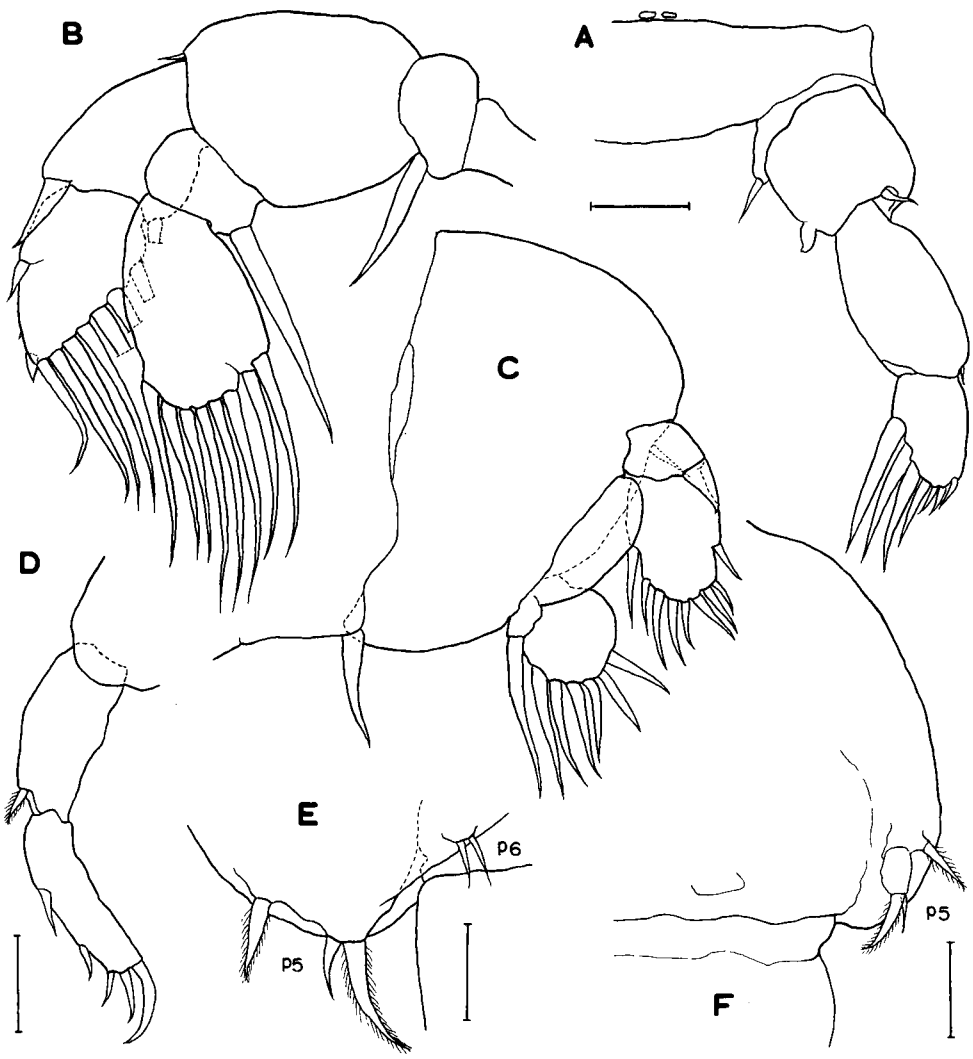

Fig. 4. *Caligus latigenitalis* Shiino, 1954, chalimus 4. A-D, first to fourth legs of male, ventral; A, forerunner of sternal furca appearing just anterior to intercoxal plate of first leg; E, posterolateral portion of genital complex of chalimus 4 male with rudimentary fifth and sixth legs, ventral; F, same portion of chalimus 4 female with rudimentary fifth leg, ventral. Abbreviations: p5, fifth leg; p6, sixth leg. Scale bars: 0.1 mm for A-D, F; 50 μ m for E.

numerals) and setae (Arabic numerals) of first three legs as follows, spines and setae all being simple and less distinguished from each other:

Leg 1	Protopod 0-1; 1-0	Exopod I-0; III, 4	Endopod 0
Leg 2	Protopod 0-1; 1-0	Exopod I-1; III, 7	Endopod 0-1; 6, 2
Leg 3	Protopod 0-1; 1-0	Exopod I-0; I, 8	Endopod 0-1; 6

Leg 4 (Fig. 4D) consisting of unimerous protopod and exopod; protopod with plumose seta at posterolateral corner, exopod with five simple elements.

Discussion

The copepodid of *Caligus latigenitalis* is almost identical with those of its congeners studied thus far (Table 1). Its body length, too, falls within their range (Table 2). The postantennary processes and the sternal processes (postoral processes) are also present in all these species. Some variations in leg armature are found among them, however, especially on the endopod of leg 1, as was pointed out by Kim (1993) and Lin et al. (1997). As seen from Table 1, the number of armature elements of the exopod is consistent among them, being eight and seven in legs 1 and 2, respectively. On the other hand, that of the endopod varies among them. The high valiability of the armature on the endopod of leg 1 may be connected with its degenerative fate in the succeeding stages. No such quantitative variation is found, however, in the counterpart stage in a sibling genus, *Lepeophtheirus* Nordmann, 1832, although the endopod of leg 1 has the same fate as in *Caligus* in the five hitherto studied species of the former genus (Table 1). In *Lepeophtheirus* the numbers of elements are consistently eight and seven on the exopod, and seven and six on the endopod, in legs 1 and 2, respectively.

Table 1. Quantitative variation of armature elements on legs 1 and 2 of the copepodids in species of *Caligus* and *Lepeophtheirus* .

Species	endopod		exopod		Reference
	leg 1	leg 2	leg1	leg 2	
C. spinosus Yamaguti, 1939	7	6	8	7	Izawa (1969)
C. punctatus Shiino, 1955	7	6	8	7	Kim (1993)
C. epidemicus Hewitt, 1971	7	6	8	7	Lin et al. (1996)
C. latigenitalis Shiino, 1954	7	6	8	7	this account
C. orientalis Gusev, 1951	6	6	8	7	Hwa (1965)
C. clemensi Parker & Margolis, 1964	6	6	8	7	Kabata (1972)
C. pageti Russell, 1925	6	6	8	7	Ben Hassine (1983)
C. labracis T. Scott, 1902	6	5	8	7	Gurney (1934)
C. maltispinosus Shen, 1957	5	6	8	7	Lin et al. (1997)
L. dissimulatus Wilson, 1905	7	6	8	7	Lewis (1963)
L. hospitalis Fraser, 1920	7	6	8	7	Ho (pers. comm.) concerning Voth (1972)
L. pectoralis Müller, 1776	7	6	8	7	Boxshall (1974)
L. salmonis (Krøyer, 1837)	7	6	8	7	Johnson and Albright (1991)
L. kareii Yamaguti, 1936	7	6	8	7	Izawa (unpublished data)

From the sizes of the chalimus larvae in the four species of *Caligus* studied thus far in which all four chalimus stages have been precisely described (Table 2), the standard growth pattern of chalimus 1-4, expressed relative to copepodid body length, is estimated to be 130-140% in chalimus 1, 180-200% in chalimus 2, 270-300% in chalimus 3, and 370-440% in chalimus 4. The identification of chalimus 2 of C. latigenitalis examined here, even though it is missing the frontal filament, can be confirmed by its body size. The body length (1.11 mm) is 202% of the copepodid body length (0.55 mm), a proportion that is reasonable for chalimus 2.

Table 2. Reported body lengths of copepodid and chalimus stages (mm) and relative body length (% compared to copepodid) in some species of *Caligus* (F, female; M, male).

Species	Copepodid	chalimus stages			
Reference		1	2	3	4
C. orientalis	0.64	0.87	1.3	1.81	F, 2.43; M, 2.63
Hwa (1965)		(136)	(203)	(283)	(380); (411)
C. clemensi	0.66	0.91	1.31	2.18*	F, 2.94; M, 3.15
Kabata, 1972		(138)	(198)	(330)	(445); (477)
C. punctacus	0.56	0.73	1.05	F, 1.39; M, 1.10	F, 1.94; M, 1.52
Kim, 1993		(130)	(186)	(290); (286)	(442); (421)
C. multispinosus	0.52	0.71	F, 0.95; M, 0.88	F, 1.39; M, 1.10	F, 1.94; M, 1.52
Lin et al., 1997		(135)	(183); (169)	(267); (212)	(373); (292)
C. latigenitalis	0.55	----	1.11	----	F, 2.45; M, 2.32
present paper			(202)		(445); (422)

*from fig. 45, wrong in text

Other stage-specific characters may also be compared among species. In *C. centrodonti* Baird, 1850 (cf. Gurney, 1934), *C. punctatus* (cf. Kim, 1993), and *C. multispinosus* (cf. Lin et al., 1997) the postantennary processes reappear in chalimus 2, but they do not do so in chalimus 2 of *C. latigenitalis* nor in *C. clemensi* (cf. Kabata, 1972); in this last species these processes reappear in chalimus 3. The two specimens of chalimus 4 of *C. latigenitalis* have frontal filaments that are quite similar to those of *C. elongatus* studied by Piasecki & MacKinnon (1993) and *C. punctatus* studied by Kim (1993). All have three extension lobes at the base of frontal filament and two pairs of connecting pads ventrally on the lobes (Fig. 3E, F). These are the diagnostic features of the chalimus 4 larvae shown by Piasecki & MacKinnon (1993) and Kim (1993). The proportional sizes of chalimus 4 (445% in the female, 422% in the male) of *C. latigenitalis* are also reasonable for this stage.

Two types of frontal filaments are found among the chalimus larvae of *Caligus* species. One type is that seen in *C. elongatus* and *C. punctatus*, which has a bulbous base, or the extension lobe(s) accompanied by connecting pad(s) ventrally (Piasecki & MacKinnon, 1993). Another type is seen in C. *spinosus* (cf. Izawa, 1969: fig. 13c), in which the newly secreted frontal filament at each stage is connected to the previous one, and extends linearly

so that no bulbous base or extension lobe(s) is formed as in the former type. In this type the frontal filament adds "segments" and increases in length with stage. It is far longer than the former type. In *C. spinosus* (cf. Izawa, 1969: fig. 13c) the frontal filament exceeds the body length and segmented. It is unknown whether these two types of frontal filament are fundamentally difference or whether the difference arises only from the condition of the newly secreted portion of the filament. In addition to *C. elongatus*, and *C. punctatus* (cf. Kim, 1993), and *C. latigenitalis* dealt with here, the elongatus type of frontal filament is found in *C. orientalis* (cf. Hwa, 1965), *C. centrodonti* Baird, 1850 (cf. Gurney, 1934), *C. labracis* (cf. Gurney, 1934), and *C. pageri* (cf. Ben Hassin, 1983), although the connecting pads were not confirmed in the last three species by the respective workers. On the other hand, *C. epidemicus* (cf. Lin et al., 1996) and *C. multispinosus* (cf. Lin et al., 1997) have frontal filaments of the spinosus type. The type of frontal filament of *C. curtus* (cf. Heegaard, 1947) and *C. clemensi* (Kabata, 1972) is unclear.

The lunules and the sternal furca of the next stage can be seen through the cuticle in advanced chalimus 4 in *C. punctatus* (cf. Kim, 1993: fig. 5), *C. multispinosus* (cf. Lin et al., 1997: fig. 1), and *C. latigenitalis* (this study). These structures and the marginal membrane of the cephalothorax are characteristic features of the adult stage. Chalimus 4 of *C. clemensi* described by Kabata (1972) is regarded here as having been in the process of molting, because the marginal membrane of the cephalothorax and the sternal furca have appeared, although the lunules are still seen beneath the cuticle. Because lunules are visible beneath the cuticle, chalimus 3 of both *C. centrodonti* and *C. labracis* described by Gurney (1934: figs.10-12) are here regarded as chalimus 4. Similary, the lunules and sternal furca are seen beneath the cuticle of chalimus 3 of *C. epidemicus* described by Lin et al. (1996: fig. 6B, G), and so this is also really chalimus 4. Fainaly, in agreement with Johnson & Albright (1991), chalimus 3 of *C. pageti* studied by Ben Hassine (1983) is here also regarded as chalimus 4 (lunules beneath the cuticle), and his chalimus 4 as the adult because of having developed lunules and a marginal membrane on the cephalothorax. Judging from overly long body of his chalimus 2 (1.65 mm from fig. 195) in comparison to those of the copepodid (0.67 mm) and chalimus 1 (0.74 mm), true chalimus 2 is seemed to have been missed by the author. Izawa (1969) described only three chalimus stages in the life history of *C. spinosus*, but he missed true chalimus 2 and his chalimus 2 and 3 are chalimus 3 and 4, respectively, as was pointed out by Johnson & Albright (1991) based upon the level of development seen in the structure of the thoracic legs.

Although a so-called preadult stage (or stages) has been inserted between chalimus 4 and the adult by many workers except Kim (1993) and Piasecki & MacKinnon (1995), the pre-adult is not a true inster accompanied by molting, but the young adult, judging from following points. The genital opercula have been completed in the preadult male and the spermatophores have begun to form beneath the opercula. The preadult female mates frequently or already has spermatophores attached to the proper site on the genital complex as seen in *C. spinosus* (cf. Izawa, 1969: figs. 17, 18), *C. clemensi* (cf. Kabata, 1972: fig. 95), and *C. epidemicus* (cf. Lin and Ho, 1993). As claimed by Kim (1993) and Piasecki & MacKinnon (1995), the stage succeeding to chalimus 4 is the adult. This is the same in

Lepeophtheirus, as seen in *L. salmonis* Krøyer, 1837 (cf. Johnson & Albright, 1991), *L. pectoralis* (Müller, 1776) (cf. Boxshall, 1974), and *L. dissimulatus* Wilson, 1905 (cf. Lewis, 1963). Although *Lepeophtheirus* species have no lunulues, the marginal membrane of the cephalothorax appears in the stage following chalimus 4, just as in *Caligus*. Thus it follows that the number of postnaupliar developmental stages is 6, including the adult, both in *Caligus* and *Lepeophtheirus*, i.e. the same as in other copepod groups including the free-living forms.

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